Current Biology 23, 1330–1334, July 22, 2013 ©2013 Elsevier Ltd All rights reserved http://dx.doi.org/10.1016/j.cub.2013.05.051

Report

Rapid Glass Sponge Expansion after Climate-Induced Antarctic Ice Shelf Collapse

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Summary

Over 30% of the Antarctic continental shelf is permanently covered by floating ice shelves [1], providing aphotic conditions [2, 3] for a depauperate fauna sustained by laterally advected food [4, 5]. In much of the remaining Antarctic shallows (<300 m depth), seasonal sea-ice melting allows a patchy primary production supporting rich megabenthic communities [6, 7] dominated by glass sponges (Porifera, Hexactinellida) [8–10]. The catastrophic collapse of ice shelves due to rapid regional warming along the Antarctic Peninsula in recent decades [11] has exposed over 23,000 km^2 of seafloor to local primary production [12]. The response of the benthos to this unprecedented flux of food [13] is, however, still unknown. In 2007, 12 years after disintegration of the Larsen A ice shelf, a first biological survey interpreted the presence of hexactinellids as remnants of a former under-ice fauna with deep-sea characteristics [14]. Four years later, we revisited the original transect, finding 2- and 3-fold increases in glass sponge biomass and abundance, respectively, after only two favorable growth periods. Our findings, along with other long-term studies [15], suggest that Antarctic hexactinellids, locked in arrested growth for decades [8, 16], may undergo boom-and-bust cycles, allowing them to quickly colonize new habitats. The cues triggering growth and reproduction in Antarctic glass sponges remain enigmatic.

Results and Discussion

Until very recently, Antarctic hexactinellids with sizes of up to 2 m [16] were considered end members of climax communities established decades to centuries after physical disturbance [17]. Slow growth and longevity in glass sponges were supported by long-term settlement studies in McMurdo Sound, where two large hexactinellid species, *Anoxycalyx* (*Scolymastra*) *joubini* and *Rossella nuda*, were reported to show no signs of reproduction or growth over a 10-year period [16]. These generalizations have been challenged by the report from the Ross Sea of a third, smaller species, *R. racovitzae* (species identification under discussion [15]), exhibiting asexual reproduction with fast growth [16], and by recent findings on artificial substrate in McMurdo Sound of massive settlement and fast growth in one of the previously nongrowing species, *A. joubini* [15]. These conflicting observations, along with the discovery of a rich benthic community thriving in total darkness under the Amery Ice Shelf, 100 km away from the ice edge [5], make it impossible to infer the dynamics of the Antarctic benthos on the basis of single observations in time, so that the interpretation of organisms present in post-ice shelf collapse surveys as recent colonizers [13] or remnant under-ice fauna [14] has so far remained an unresolved issue.

In 2007, 12 and 5 years after the disintegration of the Larsen A [18] and B [19] ice shelves, respectively, the low faunal density, low species richness, and occurrence of deep-sea taxa testified to the former oligotrophic conditions, but the presence of pioneer species such as fast-growing ascidians *Molgula pedunculata* suggested an early successional stage of the colonization process [14]. In 2011, R/V *Polarstern* revisited the Larsen area after breaking through heavy pack ice in the western Weddell Sea, one of the most inaccessible parts of the Antarctic [20]. In spite of moving ice floes challenging the umbilical cable of the remotely operated vehicle (ROV), we managed to fly it exactly on top of the 2007 Larsen A South ROV transect (Figure 1; see Supplemental Experimental Procedures available online) near the remnant strip of ice between the continent and Robertson Island.

Comparative analysis of the scaled video footage along with size-mass relationships obtained from trawl-caught sponges (see Supplemental Experimental Procedures) showed a doubling in hexactinellid sponge biomass (Table 1) and an up to 3-fold increase in their abundance (Table 2; Figure 2) after only 4 years.

The hexactinellid population at our site displayed a skewed size distribution dominated by small individuals (Figure S1). Sponges in Antarctic climax communities, by contrast, show an even size frequency distribution or are skewed toward larger individuals [8, 22]. We therefore conclude that recruitment in the Larsen area was extremely active [14], in spite of only moderate increases in local productivity [13] and an absence of large broodstock. *Rossella* cf. *villosa* (Figure S2 and Supplemental Note) was by far the most common sponge, with rare incidences of *A. joubini* and occasional *R. vanhoeffeni*. Some of the *R.* cf. *villosa* harbored numerous small spheres (diameter 1–10 mm) of sponge tissue in their spicule coats, reminiscent of sponge recruits in other species [23]. Similar features were attributed to asexually produced buds in a closely related species, *R. racovitzae* [8, 16, 22]. Pulses of food supply have been shown to foster reproduction of hexactinellids in the deep sea [24]. Spatiotemporal boosts in asexual budding and/or sexual reproduction may help explain the rapid colonization of the seafloor in Larsen A, but also the patchiness of sponge distribution (Figure 2) and population growth elsewhere in the Antarctic [15].

The sponge boost at our site, and partly also in the elevated artificial structures in McMurdo Sound [15], may be sustained by three main factors: low predation pressure, reduced competition for space and food, and increased supply of organic material.

Asteroid predators [8, 16] were scarce in both surveys (Table S1), with incidental observations of *Odontaster*

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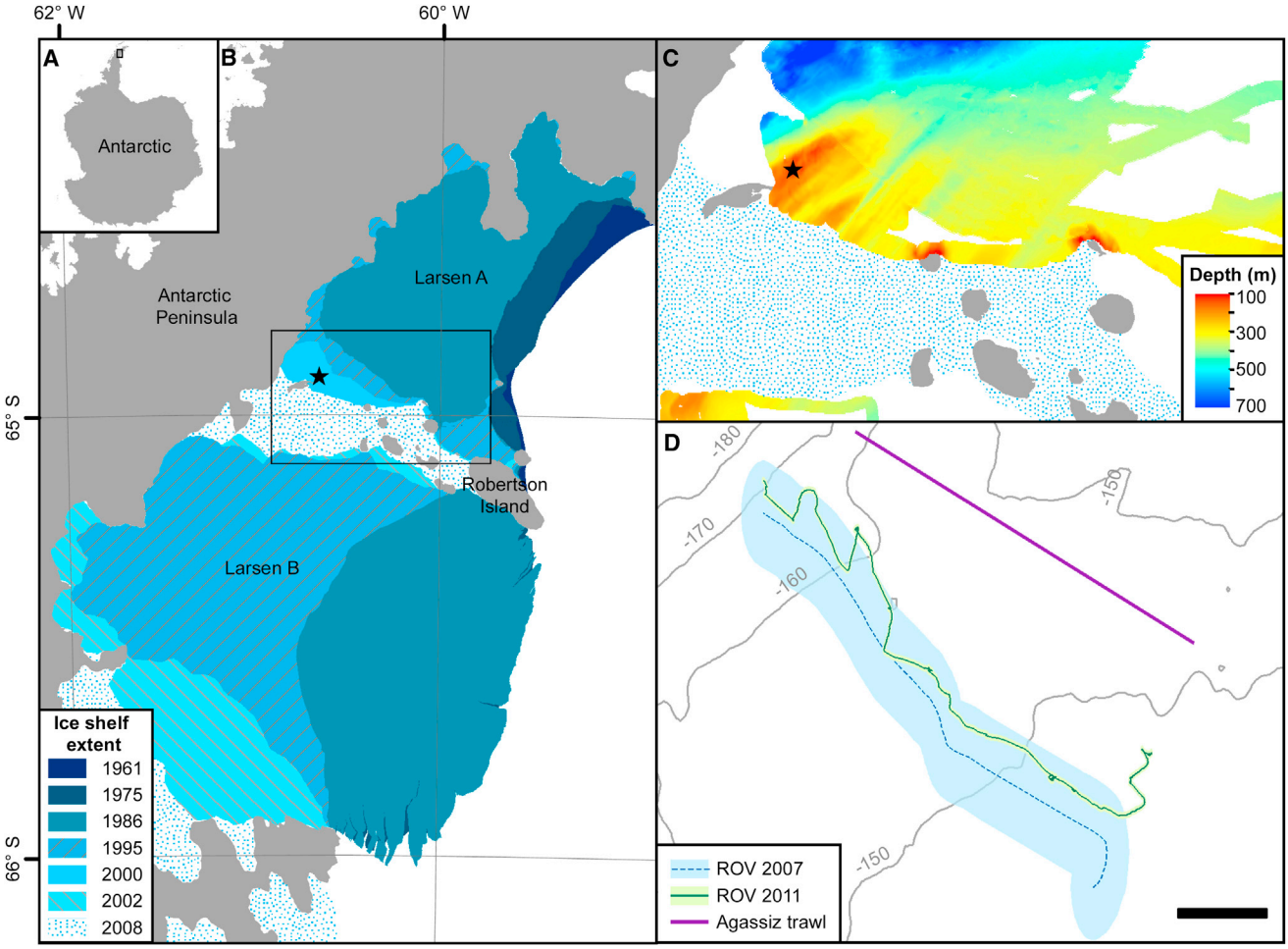

Figure 1. Study Site

(A) Location of the study site on the Antarctic continent.

(B) Larsen area, showing sequence of ice shelf collapse [11]. Black rectangle denotes study area shown in (C), with the position of the superimposed 2007 and 2011 transects indicated by the star.

(C) Bathymetry around the site. Star denotes position of the transects magnified in (D).

(D) Agassiz trawl and ROV tracks. 2007 ship track is shown as dashed blue line, with the location of the transect in a 50 m envelope around the track shown as light blue area (see Supplemental Experimental Procedures). 2011 ROV track is shown as green line; the 4 m envelope (green area) is not visible at this scale. Isobaths (gray lines) indicate depth in meters; scale bar represents 100 m.

Projection for all maps is Lambert Azimuthal Equal Area. See also Figure S3.

meridionalis attacking small *R.* cf. *villosa*. *Doris kerguelenensis*, a nudibranch preying on hexactinellids [8], was spotted only once on the 2011 transect. Thus, predation did not appear to play a significant role in sponge population control in Larsen A.

In comparison with almost total sponge cover in other parts of the Weddell Sea [25], the seafloor in Larsen A still remains far below carrying capacity. The most obvious competitors for space and food were the ascidians *M. pedunculata* and *Corella eumyota* [14], which all but disappeared from the area between 2007 and 2011 [21]. Suspension-feeding ophiuroids also decreased in number over this period and were replaced by deposit-feeding species [21].

Table 1. Glass Sponge Biomass and Production

	2007	2011
Dry mass (g/m^2)	17.5	32.5
Ash-free dry mass (g/m^2)	3.5	7.5
Carbon (gC/m^2)	1.7	3.2

See also Table S5.

Although intense phytoplankton blooms occurred in the Larsen A/B area in December 1996 [26] and in summer 2004/2005 [12], the supply of pelagic food to the benthos appears to be lower in the Larsen area than in other parts of the Antarctic [13]. Our analysis of available ice cover and chlorophyll data in the study area (Figure S3; Table S2) revealed the occurrence of phytoplankton blooms, but also large interannual differences in sea-ice and productivity: 7 of 11 summers were characterized by low sea-ice and high chlorophyll concentration, but only two vernal phytoplankton blooms occurred between 2007 and 2011. In spite of the high interannual variability and the overall low fluxes to the seafloor [13], food shortage did not appear to have interfered with the massive proliferation of glass sponges in Larsen A, supporting claims that resuspension of bed load material may play an important role in benthic trophodynamics [27]. The largest abundance increase

Table 2. Abundance Increase between 2007 and 2011

Size Class (Height × Width)	Abundance 2007 Mean ± SE (Sponges/m^2)	Abundance 2011 Mean ± SE (Sponges/m^2)	2011:2007 Abundance Ratio	Wilcoxon p Value	Permutation: Achieved Significance Level
<25 cm^2 corrected	0.54 ± 0.09	0.91 ± 0.10	1.7	<0.001*	0.0496
25–50 cm^2	0.15 ± 0.03	0.16 ± 0.02	1.1	0.407	0.0491
50–100 cm^2	0.04 ± 0.01	0.13 ± 0.02	3.0	<0.001*	0.0479
>100 cm^2	0.06 ± 0.01	0.11 ± 0.01	1.9	0.007*	0.0492
All combined	0.79 ± 0.11	1.31 ± 0.12	1.7	<0.001*	0.0497

Statistical comparison of glass sponge abundance between 2007 and 2011 for each size class. * indicates significant difference ($p < 0.01$).

occurred in the 50–100 cm^2 size class, suggesting rapid growth of juvenile sponges (Table 2). In contrast, the lack of significant change in the 25–50 cm^2 size class may be a result of interannual variability in productivity causing differential growth, recruitment, or mortality in the population.

The rapid build-up of glass sponge populations within years, rather than decades or centuries [17], suggests a much swifter response of the Antarctic benthos to a changing climate than previously assumed. If the alarming rate of ice shelf disintegration continues, with increased primary production [12] and reduced asteroid predation in response to ocean acidification [28], glass sponges may find themselves on the winners' side of climate change, enhancing pelagic-benthic coupling and silicon deposition [29] on the Antarctic shelf.

Experimental Procedures

Study Site

We used video material from two ROV dives performed at the same site in the southern portion of the Larsen A area in 2007 [14] and 2011 (Figure 1) and samples collected by trawling (details in Supplemental Experimental Procedures). This site has remained covered with ice shelf extending ~4 km northward between the major collapse in 1995 and January 2006,

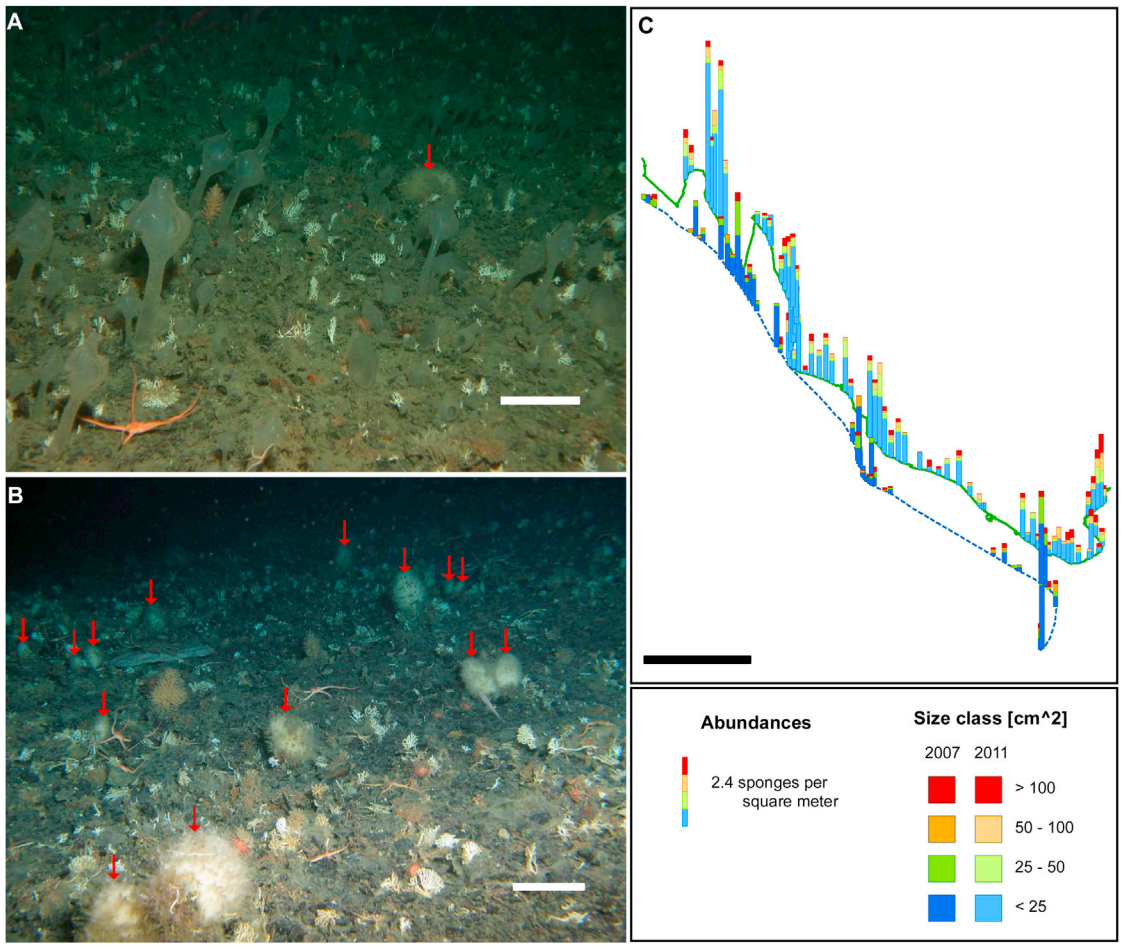

Figure 2. Glass Sponge Abundance

(A) Few glass sponges (red arrow) were seen along the 2007 transect, where the megabenthic community was dominated by fast-growing ascidians [14].
(B) Glass sponges (red arrows) dominate the 2011 transect, while the ascidians have all but disappeared [21]. Scale bars represent 10 cm.
(C) Abundances for each size class on the 2007 (dashed blue line) and 2011 (green line) transects. Scale bar represents 100 m.
See also Figures S1, S2 and S4.

when the remnant portion of ice shelf above it disintegrated (Figure S3). Along the repeat transects, the seafloor was relatively flat and composed of mud, sand, and pebbles, with regular occurrence of dropstones. Depth varied by less than 25 m, and the temperature, salinity, and oxygen concentrations recorded at the bottom in 2011 remained within 2% of the mean during the entire dive (Table S3).

Video Scaling

Three-dimensional modeling of the seafloor from the two-dimensional video data [30] allowed us to compute the dimensions of 47 subtransects for the 2007 dive, and 71 subtransects for 2011, covering a total area of 637 and 988 m^2, respectively. The surface covered by single subtransects, 13 m^2 on average, was not different between dives (two-sided Wilcoxon test, $p = 0.752$) (details in Supplemental Experimental Procedures).

Abundance

Glass sponges and asteroids were counted and measured (details in Supplemental Experimental Procedures) in the subtransects. Sponges were grouped into size classes (Figure S4; Table S4), and two-sided Wilcoxon tests were carried out to test for differences in abundance and size between 2007 and 2011. Additional permutation tests were applied to validate the consistency of the results (details in Supplemental Experimental Procedures).

Biomass

Size-mass regression analyses carried out on hexactinellids collected in the trawl showed a remarkable fit between sponge area and mass, allowing conversion of video data on sponge abundance and area to sponge biomass (dry mass and ash-free dry mass) (Table S5). These equations were used to calculate the glass sponge biomass per area for 2007 and 2011 (details in Supplemental Experimental Procedures).

Ice and Chlorophyll

MODIS and SeaWIFS satellite data were used to assess the ice cover and chlorophyll concentration in the Larsen A/B area from September 1998 through April 2012 (details in Supplemental Experimental Procedures).

Data

All primary data and statistical analyses are available at http://doi.pangaea.de/10.1594/PANGAEA.809446 (details in Supplemental External Data).

Supplemental Information

Supplemental Information includes four figures, five tables, a Supplemental Note, Supplemental Experimental Procedures, and Supplemental External Data and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.05.051.

Acknowledgments

This research was supported by the Alfred Wegener Institute (PACES T1.4, T1.6) and the University of Gothenburg. D.J. is supported by the Deutsche Forschungsgemeinschaft (JA 1063/14, 1, 2; JA 1063/17-1). We thank Julian Gutt for providing the 2007 video material, Stephan Frickenhaus for statistical support, Christian Göcke for taxonomic input, Daniel Damaske for editing the bathymetry, Mariana Altenburg Soppa for chlorophyll data conversion, Katharina Völlkopf for assistance in video analyses, Lea Krause for laboratory assistance, Ruth Alheit for the English review, and Paul K. Dayton, David K.A. Barnes, and an anonymous reviewer for their valuable contributions to the final manuscript.

Received: April 15, 2013
Revised: May 24, 2013
Accepted: May 28, 2013
Published: July 11, 2013

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